

Royle NJ, Hartley IR, Parker GA. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol Evol.* 17: 434–440.

## On the meaning of hunger and behavioral control in the evolution of honest begging

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Mock et al. (2011) in the following referred to as “MDS”, point out some weaknesses and inconsistencies in begging research, and they convincingly place signaling of need (Godfray, 1991) and signaling of quality (Grafen, 1990) at eye level as 2 competing hypotheses for the evolution of offspring begging signals. Hopefully, the 2 hypotheses will be placed to balanced tests in the future.

They further point out that the widespread hunger experiments are not tests of signals of “need” as envisaged by Godfray (1991) (see Royle et al. 2002 for previous, albeit different, criticism) because hunger is a poor predictor of offspring fitness returns on investment. They propose instead to treat hunger-dependent begging as conceptually separate proximate “signals of hunger.” The relation between proximate control of begging by hunger and ultimate causes of condition dependence of begging by need/quality is critical and possibly also at the heart of some of the confusion surrounding the concept of “need”, I agree. However, I don’t think hunger effects on begging are as detached from evolutionary theory as the authors suggest. Godfray (1991) and others assumed in their models a single begging–provisioning interaction between an offspring and a parent. Under such simplistic conditions, more hungry offspring would actually often stand to gain more in terms of fitness from the single expected provisioning, and hunger would be a useful proxy for need. The core limitation of hunger as operational definition for need in experimental research is the characteristic repetitiveness of parent–offspring interactions in nature. The highly dynamic nature of hunger effects on offspring begging, begging effects on parental provisioning, and provisioning effects on offspring hunger makes hunger a highly transient state, concealing in very short time any potential relation between hunger and offspring fitness gains.

But even then, we don’t have to exile hunger effects on begging to a purely proximate realm. Hunger experiments measure how offspring behaviorally react to variation in food provisioning at a given moment in time (Kölliker 2003). This causal relation was termed “effect of supply on demand—or ESD—mechanism” (Mock and Parker 1997; Parker et al. 2002; Kölliker 2003) or “demand reaction norm” (Smiseth et al. 2008). The slope of the demand reaction norm describes how begging encodes information about variation in recent food intake and comprises the proximate mechanisms that translate food intake into variation in begging (e.g., digestive efficiency, genetic variation, hormonal or ontogenetic changes; see Wright and Leonard 2002). Together with the parental supply reaction norm, the demand reaction norm determines the levels of provisioning and begging in the repeated interactions (Kölliker 2003) and plays a role in mediating the behavioral dynamics between parents and offspring (Dobler and Kölliker 2009). Finally, like reaction norms in general, the demand reaction norm is

a potentially heritable and evolving trait (Smiseth et al. 2008), maybe even one of key interest in the evolution of family interactions.

Thus, I would not go so far as to request a “moratorium on the hunger experiment” (MDS). Hunger experiments are often (and reasonably) the first step into the study of parent–offspring interactions in less well-studied organisms in which begging is not as obvious to the human observer as in birds. In such systems, they remain an essential tool to identify candidate begging traits. Furthermore, the “at least as an end to itself” part in MDS’s proposal seems essential to me, although the authors do not elaborate on it. Little is known about causal agents of interindividual variability in demand reaction norms or how selection operates on them. For example, is there heritable variation, ontogenetic shifts, and growth/learning/environmental effects on the slope of the demand reaction norm? Is the demand reaction norm expected to evolve differently if begging evolves as a signal of need as opposed to a signal of quality or as a means of scramble competition? Does sibling rivalry select for more or less hunger-sensitive begging? Such questions have not been broadly enough studied—neither theoretically nor experimentally. In my opinion, hunger experiments should continue to play an important role in research on begging but properly applied and interpreted: Hunger may usually not reflect need. The hunger effect on begging is a measurement of an offspring trait—the slope of the demand reaction norm.

Most scientists in the field probably would agree with MDS that testing for behavioral control (bc) is of prime importance in future research on begging (Royle et al. 2002). Theoretically, bc is a model assumption needed to define which party makes active choices, that is, to which degree parents impose selection on offspring or vice versa. However, empirically, it is not so obvious what kind of trait bc should be and how we should test or observe this potentially cryptic trait. As a cautionary note, the term shares some of the properties that rendered need ambiguous and misleading. Like need, “bc” is theoretically straightforward, intuitively appealing, and empirically difficult to grasp, test, and quantify. While I agree with MDS that careful observation is essential, I doubt that observation alone will be sufficient in many cases. Manipulative experiments will be required to causally disentangle bc and to generalize beyond the limits of the behavioral repertoire of a given species [see Hinde et al. (2010) for an approach to disentangle bc based on co-adaptation logic]. I think this will be important to avoid erroneously assigning bc based on easily observable behaviors that are interpreted as control behaviors on intuitive grounds.

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